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THE POTENTIAL USE OF THE PARASITES *Crassicauda* (Nematoda) AND *Nasitrema* (Platyhelminthes) AS BIOLOGICAL TAGS AND THEIR ROLE IN THE NATURAL MORTALITY OF COMMON DOLPHINS, *Delphinus delphis*, IN THE EASTERN NORTH PACIFIC

by

William A. Walker, F. G. Hochberg
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ADMINISTRATIVE REPORT LJ-84-08C

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THE POTENTIAL USE OF THE PARASITES CRASSICAUDA (NEMATODA) AND NASITREMA (PLATYHELMINTHES) AS BIOLOGICAL TAGS AND THEIR ROLE IN THE NATURAL MORTALITY OF COMMON DOLPHINS, DELPHINUS DELPHIS, IN THE EASTERN NORTH PACIFIC

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May 1984

This report was prepared by William A. Walker, F. G. Hochberg, and Elizabeth S. Hacker under contract No. NOAA/82-ABC-00042 for the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California. The statements, findings, conclusions and recommendations herein are those of the author(s) and do not necessarily reflect the views of the National Marine Fisheries Service. William F. Perrin of the Southwest Fisheries Center served as Chief Official Technical Representative for this contract.

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INTRODUCTION

This study surveys the incidence of the platyhelminth *Nasitrema* sp(p). and the nematode *Crassicauda* sp(p). in the air sinus and inner ear complex of the common dolphin, *Delphinus delphis* in the eastern North Pacific. Primary areas of investigation involve the potential use of these two parasites as natural biological tags in stock separation and their role in the natural mortality of free ranging populations.

The spirurid nematode genus *Crassicauda* is associated with the natural mortality of the spotted dolphin, *Stenella attenuata*, in the eastern tropical Pacific (Dailey and Perrin, 1973). Perrin and Powers (1980) projected age-related natural mortality rates for *S. attenuata*, based upon the incidence of *Crassicauda*-induced skull lesions among museum specimens. Walker and Cowan (1981) demonstrated a similar age-related incidence of *Crassicauda* in three eastern North Pacific populations of *Delphinus delphis*.

Species in the digenean genus *Nasitrema* infect a wide variety of small toothed whales in the North Pacific. Although originally described from the western Pacific, (Ozaki, 1935; Yamaguti, 1950) the genus is also common in cetaceans throughout the eastern Pacific from California to Panama. At present the descriptive literature is sparse. With the exception of *N. attenuata* and *N. globicephalae*, most species are not well defined.

Nasitrema sp(p). normally live in the maxillary and pterygoid sinuses of small cetaceans. They are also known to invade the inner ear (Dailey and Ridgway, 1976; Parker et al., 1977). Though generally considered harmless, the presence of large numbers of worms may induce chronic sinusitis (Sweeney and Ridgway, 1975) and severe tissue damage (Walker and Cowan, 1981). In addition, species of *Nasitrema* have repeatedly been documented to invade the cranial vault and migrate through the brain tissue. Resulting pathology of the central nervous system may eventually contribute to the stranding and/or death of the host (Cowan et al., in press; Dailey, 1978; Dailey and Walker, 1978; Johnston and Ridgway, 1969; Parker et al., 1977; Ridgway, 1979; Ridgway and Dailey, 1972; Ridgway and Johnston, 1965). Kumar and coworkers (1975) reported that continued aspiration of *Nasitrema* eggs deep into the lungs of captive animals may provoke pneumonic conditions leading to stress and/or death or the host.

The incidence of *Nasitrema* in stranded *Delphinus delphis* along the southern California coast is very high. The density of worms in the air sinus complex may number in the hundreds and extensive pathology is frequently evident (Cowan et al., in press). The consistent association of *Nasitrema* with stranded *D. delphis* prompted an initial study on free ranging populations (Walker and Cowan, 1981). Preliminary observations suggested that two or possibly three morphotypes of *Nasitrema* were present in the samples they examined and indicated that several species may be involved. The current study utilizes and elaborates on the samples collected for the above report. The question of species identification and the potential of using species of *Nasitrema* as biological tags is examined.

In order for a parasite to be considered as a potential biological tag in stock identification the following criteria (adapted from Mackenzie, 1981, in press) should be met:

- The parasite must have significantly different levels of infection in host populations within different geographical regions.
- The parasite should have little pathological effect on the host. A highly pathogenic parasite may cause selective mortality or behavioral changes in infected hosts.

- Ideally the parasite should be easily seen, recovered and identified. Since large numbers of hosts and parasites often have to be examined, methods which involve extensive dissection, complicated preparations or time consuming microscopic examinations should be avoided.
- The parasite must have a life span (or remain in an identifiable form) in the host long enough to cover the time scale of the investigation.
- For stock separation, parasites with single-host life cycles are the simplest to use. Parasites with complex life cycles involving two or more hosts require a great deal of background ecological information before they can be used as effective tags.

The use of parasites as biological tags to identify stocks of dolphins in the eastern North Pacific has only recently undergone investigation. Differences in parasite faunas were noted for stocks of bottlenose dolphins, *Tursiops truncatus* (Walker, 1981), and common dolphins, *Delphinus delphis* (Walker and Cowan, 1981). In a third study Dailey and Otto (1982) suggested that parasites may prove useful as tags for striped dolphins, *Stenella coeruleoalba*, pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and common dolphins, *D. delphis*.

MATERIAL AND METHODS

A. *Crassicauda*

Specimens were examined for evidence of the characteristic, *Crassicauda*-induced lesions illustrated in Dailey and Perrin (1973). Data on number, size and location of parasitic lesions also were recorded.

A total of 521 prepared crania were available for examination. Three recognized subpopulations or stocks of *Delphinus delphis* were represented in the sample. Terminology and geographic delineation of stocks follow that presented in Perrin et al., (1983).

1. Central Common Dolphin: 171 specimens taken incidentally in the yellowfin-tuna purse-seine fishery between latitudes 5°03′N to 10°36′ and longitudes 83 °13′W to 95°22′W.
2. Northern Common Dolphin: 255 crania were examined. A total of 188 specimens were collected at sea, of which 61 were taken in the yellowfin-tuna purse-seine fishery in the southern area (at approx. 20°N) and 127 were collected in the southern California area (at approx. 32-33°N) either for live display or research purposes. Sixty seven (67) specimens were collected as single strandings occurring from central California (approx. 37°N) south to southern California (approx. 32°N).
3. Baja Neritic Common Dolphin: 95 cranial specimens collected along the immediate coastline throughout the Gulf of California and west coast of Baja California, Mexico. The majority (92 specimens) are beach worn skulls, which probably represent mortality due either to strandings or local shore-based fisheries activiites. Only three specimens represent live collections.

The distributional ranges of the Baja neritic and northern common dolphins exhibit considerable overlap (Evans, 1975; Perrin et al., 1983). Samples collected from the Mexican coast consisted primarily of beach worn skulls. Little associated length, sex or color pattern data on individual specimens were available. We elected to follow Banks and Brownell (1969) and Evans (1975) and conservatively selected only those cranial specimens exhibiting rostral length-zygomatic width ratios of 1.60 or greater as having a high probability of being representative of this subpopulation. This criterion reduced the sample of Baja neritic common dolphins to 59 specimens.

B. *Nasitrema*

The air sinuses of 104 specimens were examined for *Nasitrema*. Of these, 101 were collected in 1977 and frozen prior to examination and three were collected in 1978 and examined while still fresh. Dolphin hosts representing three described stocks (see above) were taken as incidental catches in commercial tuna fishing operations and were obtained through the Southwest Fisheries Center.

Walker and Cowan (1981) briefly described the removal and initial fixation of *Nasitrema* samples. With the excepiton of the three samples discussed, all worms were extracted from *Delphinus* heads which had been frozen in the field. Prior to examination the heads were thawed. Loose worms were flushed from the air sinus and inner ear complex with moderate water

pressure. When necessary, embedded worms were excised from the tissue in order to obtain total counts. Following removal all helminiths were fixed in 4% buffered formalin and later transferred and preserved in 70% ethyl alcohol. No worms were relaxed prior to fixation, nor were any worms flattened during the process of fixation. In the case of three dolphins taken in 1978, (WAW 589-591) parasites were removed from recently dead hosts and fixed in formalin while still alive.

Nasitrema samples from 89 infected spcimens of *Delphinus delphis* were available for study (see Appendix I). The host sample consisted of 47 female and 42 male dolphins, ranging in length from 155 to 236 cm. A total of 1806 individual worms were measured using a dissecting microscope. In each sample only intact, entire worms were measured. Figure 5 illustrates the principal measurements recorded, namely: total length, hindbody length, body width (at level of ventral sucker), ventral sucker diameter and body depth or thickness. Lines were drawn with the aid of a camera lucida to encompass the desired measurements and were then later enumerated with a planimeter. Outline sketches were made of select worms in most samples to record body shapes and proportions. Samples with only a single worm or samples in which one or no intact measurable worms were present were not included in Figure 6.

Nasitrema specimens from select samples were prepared for specific identification. These specimens were stained in Van Cleave's, cleared in clove oil or dioxane and mounted in histoclad for examination under the compound microscope.

Data sheets and all *Nasitrema* samples are archived in the Department of Invertebrate Zoology at the Santa Barbara Museum of Natural History.

RESULTS

A. *Crassicauda*

Crassicauda-induced bone lesions were present in varying frequency among all three subpopulations of *Delphinus delphis* surveyed.

The Baja neritic sample is, with few exceptions, almost totally devoid of specimens with accompanying length data. *Crassicauda* lesions were present in eight of the 59 specimens with rostral length - zygomatic width ratios of 1.60 or greater (overall infection rate of 13.5%.

The northern and central common dolphin populations (see Figures 1 and 2) demonstrated a similar pattern of infection to that reported for *Stenella attenuata*, where the incidence decreases with age (using size as an indicator) of the host (Dailey and Perrin, 1973; Perrin and Powers, 1980).

Differences in infection rate between the central and northern common dolphin populatons are apparent from the data presented (Figures 1 and 2). However, due to field collection criteria the number of juvenile-size-class specimens are underrepresented in the central common dolphin sample. Heads were collected primarily from animals of adult (sexually mature) size. Due to this sample bias, the validity of the differences in infection rate between the two stocks is difficult to assess. It is apparent, however, that *Crassicauda* sp(p). is present in all three populations examined and consequently unreliable as a biological tag.

Walker and Cowan (1981) presented *Crassicauda*-infection-rate data in a comparable size-stratified sample of central common dolphin collected from the same general area. Although the pattern among juveniles was similar, the overall incidence of infection was much higher (34.9%) than that observed in this study (5.8%). However, significant differences in method of examination exist in the two studies. Cowan and Walker (1981) dissected frozen heads for evidence of intact specimens of *Crassicauda*. This study examined museum cranial specimens for *Crassicauda* bone lesions. Walker and Cowan (1981) made the observation during their study that the presence of *Crassicauda* was not always associated with cranial bone lesions. The disparity in rates of infection between these two studies seems to support their observations.

Due to the potential bias in the northern common dolphin sample, the stranded sample was treated separately from those specimens collected at sea. The comparison revealed surprising results. Only one animal was infected (1.5%) in the stranded sample. In the live-capture sample, 26 animals (13.8%) were infected (see Figures 2 and 3). Comparison of the length-frequency histograms for both the stranded and live capture samples reveals that juvenile-sized individuals are underrepresented in the stranded sample. In order to determine if selectivity toward collection of adult specimens existed in museum collections, we plotted length frequency for all *Delphinus delphis* stranded in the immediate vicinity of Los Angeles, California for the years 1970-1074. This four-year period was one intensive data and specimen collection efforts in this area (Cowan et al., in press). Comparison of these data with the museum specimens collected north of 32°N reveals a similar pattern in length-frequency distribution (see Figures 3 and 4) and indicates that the underrepresentation of juvenile-sized animals is a natural phenomeon in the stranded sample.

Parasites are well known agents of selective mortality regulating host population structure as well as influencing competition of populations within ecosystems (Holmes and Bethel 1972; Holmes 1976; and Holmes 1979). Holmes and Bethel (1972) advanced the concept of parasite-induced behavioral modification resulting in host susceptability to predation. Their study, however,

dealt primarily with predator-prey interaction with intermediate hosts and the subsequent effects on parasite and host communities. *Delphinus delphis* is the definitive host for *Crassicauda* sp(p). and therefore does not ideally fit their predator-prey model.

Slobodkin (1968) suggested that the ideal predator should concentrate primarily on those members of a prey population that are the most expendable. The high *Crassicauda*-infection rate in juvenile specimens of *Delphinus delphis* and the infrequent stranding of infected juveniles in southern California suggests that this parasite may be involved in selective mortality resulting in higher predation among juvenile age classes and would account for the underrepresentation of juveniles in the stranded sample

As has been discussed, strandings of several species of small cetaceans, including those of *D. delphis*, are documented to be the result of pathology of the central nervous system related to the trematode, *Nasitrema* (Cowan et al., in press; Dailey and Walker 1978; Parker et al., 1977; Ridgway and Dailey 1972). Most of the specimens of *Delphinus delphis* occurring as individual strandings in the immediate vicinity of Los Angeles County during the 1970-1974 period were either collected alive or estimated to have stranded alive prior to collection. Pathologic effects of *Nasitrema*-induced brain lesions are frequently of long duration, and, rather than resulting in a direct cause of death, they are estimated to cause disorientation of the animals which subsequently strand and die of exposure. (Cowan et al., in press).

We suggest that the singly stranded sample of the northern common dolphin stock is not representative of all natural mortality factors involved in the population as a whole. The stranded sample probably represents and is indicative of mortality and disease factors in the older age classes of common dolphins in this area.

B. *Nasitrema*

1. *Incidence of infection*

In order for *Nasitrema* to serve as a useful biological tag, the incidence of infection should vary from region to region. In Tables I and II the incidence of infections in stranded and free ranging common dolphins *Delphinus delphis*, are arranged by latitude. Throughout the latitudinal range of the samples examined from 06° to 34°N the incidence is uniformly high, ranging from 73 to 100%. The overall high incidences observed in animals examined in this study are not significantly different from one another nor are they different from the incidences observed in stranded animals examined along the California coast (see Table I). The general trend shows a slight decrease in incidence to the south and to the west (away from the coast) which may indicate that the source of infection is tied to coastal waters. (See Table II).

The ubiquitous presence and high incidence of Nasitrema sp(p). throughout the range of a number of stocks of *Delphinus delphis* precludes the use of species of this parasite genus as biological tags.

Contrary to Dailey and Otto (1982), available literature indicates the absence of *Nasitrema* in cetacean hosts stranded in Oregon (see Dailey and Stroud, 1978; Stroud and Roffe, 1979). If this is the case, then the presence or absence of *Nasitrema* perhaps may be used in assessing stocks on a broader geographic perspective.

2. *Species Identification*

Nasitrema parasites can be easily identified to genus on the basis of their large size and location in the host. However, the species are not so easily recognized.

The status of taxa in the genus *Nasitrema* is currently unresolved. Neiland and coworkers (1970) recognized nine species in the genus (four in the western Pacific and five in the eastern Pacific) based on very small sample sizes. Using a larger series of worms collected from six species of hosts, Appy (1974) reevaluated the species of *Nasitrema* in the eastern Pacific. On the basis of his work he considered *N. stenosoma* to by synonymous with *N. globicephalae*. He later concluded (pers. comm.) that *N. delphini* and *N. laceolata* also are probably synonyms of *N. globicephalae* and that only two species exist off California, namely *N. attenuata* and *N. globicephalae* (see also Dailey and Otto, 1982). These species are distinguished principally on the basis of the following characters:

Character	*N. attenuata*	*N. globicephalae*
length, mm (mean)	19-23 (21)	9-22 (15)
shape	narrowly lanceolate	broadly lanceolate
testis	weakly lobed	strongly branched, dendritic
ovary	2-4 blunt lobes	5-10 blunt lobes
vitellaria	not extending anterior of testes	pretesticular

Walker and Cowan (1981) indicated that several morphotypes appeared to be present when they examined worms for their report. In order to be useful as an effective biological tag a parasite should be easily identified. In the past, size (length) and shape often have been relied upon a determine the various species of *Nasitrema*. Since size and shape can be quickly and routinely assessed, in a short term study of this sort these characters are the easiest and most logical ones to analyze.

a. *Size*. As indicated above, the mean and total length of *Nasitrema globicephalae* and *N. attenuata* are distinctly different, and hence it should be possible to analyze length as one element in species determination. In Figure 6, all hosts are arranged in sequence by descending latitude and are identified by sample number. The ranges and means of all worms measured in each sample are indicated. In cases where only two worms were present in a sample, the mean is not given. All cases in which only one intact worm was available are not included. The type of line indicates the sex of the host. Infections in which over 100 worms were present are indicated by an asterisk, and an arrow indicates samples that were stained and identified by microscopic examination (see also Appendix I).

Superimposed over the length plots in Figure 6 is the size range of adult *Nasitrema globicephalae* based on literature reports (Appy, 1974; Neiland et al., 1970). Although the range of worm lengths varies considerably, in a number of cases falling outside the known range of *N. globicephalae*, in only a few instances do the means fall outside this field. Most worms which measured less than 10 mm were determined to be immature (i.e. juveniles without eggs); with the exception of three principal outliers. Samples WAW 589-591 were fixed while still alive. The worms in these samples are maximally contracted and, as a consequence, appear short and fat. When critically examined the worms in these three samples were identified as *N. globicephalae*. On the basis of length it would appear that worms in all samples are typical of *N. globicephalae*.

Although the size ranges in Figure 6 are extremely variable, upon closer examination a geographical difference in mean length is suggested. Worms recovered form central common dolphins in the region of 07° to 09°N latitude appear to be longer than worms from hosts captured to the north and south. On the other hand, densities seem to be greater in the regions to the north and south, and, since density is known to affect size, this was analyzed by graphing mean worm length as a function of worm density (Figure 6). Although parasite length appeared to be inversely correlated with density, the trend was very weak. Hence, high densities seen in hosts from 06°and 22°N latitude might produce stunted worms whereas low densities which are characteristic of infections in the region from 07° to 09°N latitude would encourage larger and more robust individuals. This would have to be verified with additional samples but it indicates that parasite density may influence worm length.

A second factor which affects length is the condition of the worm at the time of fixation. The worms analyzed in this study were not uniformly relaxed, flattened and fixed immediately upon capture of the host while the parasites were still alive. In the samples at hand, length cannot be relied upon to separate species of *Nasitrema*.

b. *Shape*. Although three morphotypes were encountered in the samples examined, an analysis of shape did not indicate specific patterns which could be associated with distinct species (see Figure 7). The morphotype shown in Figure 7A is represented solely by worms in samples WAW 589-591 mentioned above. These worms were fixed fresh, hence, the squat, plump shape is an artifact of fixation. When stained and identified all three outlier samples fit the description of *Nasitrema globicephalae*. The remaining two morphs might tenatively be identified as *N. attenuata* (Figure 7B) and *N. globicephalae* (Figure 7C). However, when the remaining samples were examined most contained a mixture of the two shapes and a complete range of intergrades between the narrowly and broadly lanceolate forms.

As in size, variations in the condition of the worm samples at the time of fixation and the density of the infection may dramatically affect the shape. These characters should not be relied upon for species identification.

c. *Identification.* In order to verify the identifications, select *Nasitrema* samples were identified to species as indicated by the arrows in Figure 6 (see also Appendix I). Due to time constraints only eight samples were stained, mounted and critically examined under the compound microscope. All fit the description of *N. globicephalae* on the basis of the internal characters listed above, but principally on the basis of the anterior extent of the vitellaria. The observed plasticity in size and shape most likely is correlated with fixation and/or density of the infection.

In general, worms that have been frozen and then fixed to formalin are poor specimens for critical examination. Either the internal organs (testes and ovaries) begin to degenerate before fixation, or a white precipitate develops during processing which obscures internal details.

3. *Intensity of Infection*

Most studies of this sort record only the presence or absence of parasites, since density or number of parasites per host is not generally considered an important criterion for evaluating the tag potential of a parasite. However, since this information was available it was summarized along with incidence. This aspect proved to be one of the most interesting elements of the study, principally because *Nasitrema* species are such large and conspicuous parasites and one can be reasonably confident in recovering all the worms from a given host.

The evidence indicates that stranded dolphins (Table I) have a higher mean density of parasites than do free-ranging dolphins (Table II). Secondly, in free-ranging dolphins lower densities of *Nasitrema* are encountered in central common dolphins but only in the latitudinal range from 07° to 09°N (Table II).

In an attempt to explain the pattern of densities observed, we examined collection or station data recorded at the time of capture. Table III analyzes: a) dates of capture, b) distance of capture from shore, and c) depth of capture relative to submarine topography. From this table it is evident that dolphins captured in relatively shallow neritic water over or at the edge of the continental shelf have higher densities of parasites when compared with dolphin hosts captured in deeper off-shore waters.

A number of possibilities may explain these intensity differences.

a. Seasonal Difference in Capture: high densities of parasites may occur if there is a seasonal pulse in infection. If a seasonal pattern were present it would be indicated by the presence of large numbers of immature worms in hosts caught at specific times or seasons of the year. As indicated in Table III, with the exception of samples taken in April at 06°N latitude, the majority of collections were taken in the months of July and August. Hence, a seasonal component does not seem to be present. High numbers of immature worms present in the sample from 06° and 22° to 23°N latitude (see Figure 6) suggest that infections are not seasonally restricted.

Seasonal patterns can be ruled out as well on the basis of the longevity of the parasites. Walker (1975) recorded the presence of *Nasitrema* in a northern right whale dolphin, *Lissodelphis borealis*, which had been held

in captivity for 15 months prior to death. This animal was fed entirely on frozen food with no means of acquiring additional parasites while in captivity. Hence, individuals of *Nasitrema* live at least 15 months.

b. Age Related Differences: it is well documented that the number of parasites may vary with the size or age of the host. Older (or larger) hosts may accumulate more parasites than do younger (or smaller) hosts simply because they have been exposed to infection over a longer period of time. In other instances, hosts of a specific age may acquire higher densities of parasites through selective ingestion of infective stages which occur in intermediate hosts concentrated in their diet. To examine this hypothesis, the length (used as an index to age) of all infected and uninfected dolphins was graphed and compared latitudinally. Unfortunately, a stratified sample of adequate size was not available in the study areas. However, there is inference that age is not a factor in determining density.

c Sex-Related Differences: in some circumstances the density of parasites may be directly correlated with the sex of the host. This typically results from a feeding bias whereby one sex ingests more infective stages by selectively consuming prey which serve as intermediate hosts. If a feeding bias existed it would be reflected in higher densities in one or the other sex.

Walker and Cowan (1981) indicated that only males in the central tropical sample carried high loads (over 100 worms) of *Nasitrema*. This pattern does not appear to hold throughout the range (see Table III) although there are problems with low sample sizes in the northern and Baja neritic stocks. At 23°N latitude females have a mean number of over 100 worms when compared with males, whereas at 06°N the reverse is true. At 22°N latitude, the numbers of worms in both male and female hosts are low and there are no differences between sexes.

d. Capture Locality Differences: as a final effort to understand the observed parasite density patterns, the locations of all dolphin captures were plotted. Distance from the nearest point of land in and of itself does not appear to be correlated with the intensity of the infections observed. However, depth, which is a function of distance from shore, does appear to be a significant factor. Dolphins taken in waters over or on the edge of the continental shelf were the only ones which exhibited high-density infections (over 100 worms). The intensity of infections dropped significantly to the west. Dolphins taken in the central region from 07° to 09°N latitude were captured in deep water at a distance of 100 to over 700 km from shore and none had densities of over 100 worms.

These data suggest the presence of a "shelf effect" which might be useful in distinguishing inshore from offshore populations of *Delphinus delphis*. However, comparative offshore samples from 06° and 22° to 25°N need to be examined to verify this hypothesis. It is most likely that inshore (neritic) and offshore (oceanic) populations have different feeding habits and as a consequence are exposed to higher or lower abundances of the intermediate hosts of *Nasitrema*.

Appy (1974) concluded that the presence of large number of immature parasites in cetaceans stranded in Califonria indicated a local focus for infections of *Nasitrema globicephalae*. In the current study immature worms were commonly encountered in dolphins captured in neritic waters at 06°, 22° and 23° North. This suggests that inshore areas in the eastern tropical Pacific are also key sites for infections and supports the contention that there is a "shelf effect."

SUMMARY

The air sinus parasites *Crassicauda* sp(p). and *Nasitrema* sp(p). were surveyed from common dolphins, *Delphinus delphis,* in the eastern North Pacific for their potential use as biological tags for stock separation and their role in natural mortality. The main points are summarized as follows:

1. *Crassicauda* sp(p). is considered inadequate as a biological tag for *Delphinus delphis* in the study area. Parasites of this genus occur in all three subpopulations examined.

   Due to collection bias in the central common dolphin sample and the lack of adequate length data in the Baja neritic sample, comparison of frequency of infection between the three sub-populations is difficult to assess.

2. *Crassicauda* appears to play a role in the natural mortality of juveniles in the central and northern common dolphin populations. Length-frequency histograms of the presence of *Crassicauda*-induced lesions in *Delphinus delphis* displays a pattern similar to that demonstrated for *Stenella attenuata* in the eastern tropical Pacific. The rate of infection, as evidenced by bone lesions, decreases with age of the host.

   Comparison of *Crassicauda*-induced bone lesions in museum specimens with the findings of Walker and Cowan (1981), support their observations that the presence of this parasite is not always associated with bone lesions.

3. The stranded sample of the northern common dolphin population is not representative of all natural mortality and disease factors influencing the population as a whole.

   While mortality associated with *Crassicauda* infections is high among juveniles in the free-ranging population, juvenile-sized dolphins are naturally underrepresented in the stranded sample.

4. Distinct morphotypes or species of *Nasitrema* could not be distinguished on the basis of length or shape. All parasites examined were identified as *N. globicephalae.* The principal cause of variation in size and shape appears to be due to variations in condition of the specimens at the time of fixation, although density of parasites in the host's air-sinus complex may also influence these two characters.

5. Incidence in free-ranging and stranded dolphins from 06° to 34°N latitude is uniformly high, and hence this character can not be used to distinguish stocks. If *Nasitrema* does not extend north of 35°N then the presence or absence of the parasite may possibly be used as a tag on a broader geographical scale.

6. Intensity of infection appears to decrease to the south and to the west (away form the coast). The latter implies a "shelf effect." The presence of large numbers of immature parasites in hosts captured in neritic waters supports this suggestion and indicates that natural foci for infections occur in shallow water over the continental shelf. A discrete inshore subpopulation of *Delphinus delphis* may be suggested on the basis of parasite densities, and it may be a function of the feeding regime of animals which occur in inshore waters all along the coast.

ACKNOWLEDGEMENTS

The following institutions and staff contributed to this study: American Museum of Natural History; California Academy of Sciences; Los Angeles County Museum of Natural History; Santa Barbara Museum of Natural History; San Diego Museum of Natural History; U.S. National Museum; and the Museum of Vertebrate Zoology at Berkeley. We give special thanks to the following people for their time and consideration: Ray Bandar, CAS; Dr. Ray Gilmore, SDMHN; Robert Jones, MVZ; Dr. James Mead, USNM; Dan Russell, AMNH; Jacqueline Schonewald, CAS; and Dr. Charles Woodhouse, SBMNH.

Dr. Robert Overstreet graciously provided space and comparative *Nasitrema* material in his Department of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi. Ronnie Palmer of the same laboratory stained and mounted select helminths for examination. Laurie Marx measured worms and prepared all figures and tables. Without her assistance this report could not have been completed.

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TABLE I. Summary of Nasitrema infections in stranded common dolphins collected off Oregon and California.

STOCK	LATITUDE	TOTAL NO. EXAM.	NO. INFECT.	INCIDENCE	MEAN NO. WORMS	RANGE	REFERENCE
NORTHERN	Oregon	1	0	0%	----------	----------	Dailey & Stroud (1978)
NORTHERN	34°	7	7	100%	----------	----------	Ridgeway & Dailey (1972)
	34°	30	29	97%	----------	----------	Cowan et al (in press)
	34°	4	4	100%	234	95-466*	Appy (Ms.)
	34-33°	31	26	84%	----------	----------	Dailey (1978)
	?	15	15	100%	----------	----------	Ridgeway (1979)

* represents minimum counts

TABLE II. Summary of Nasitrema infections in free-ranging common dolphins captured in the eastern North Pacific off Mexico, Costa Rica and Panama.

STOCK	LATITUDE	TOTAL NO. EXAM	NO. INFECT.	INCIDENCE	MEAN NO. WORMS	RANGE
BAJA NERITIC	25°	2	2	100%	130	49-211
NORTHERN	23°	5	5	100%	89	9-205
	22°	11	9	81.8%	113	42-203
CENTRAL	09°	11	8	72.7%	9	1-18
	08°	47	39	82.9%	11	1-78
	07°	16	15	93.7%	16	1-65
	06°	12	11	91.6%	111	2-405
TOTALS		104	89			

dolphins captured in the eastern North Pacific off Mexico, Costa Rica and Panama.

STOCK	LATITUDE	NASITREMA				DATES OF CAPTURE	KM OFFSHORE	DEPTH
		NO. ♀ INFECT.	MEAN NO. WORMS	NO. ♂ INFECT.	MEAN NO. WORMS			
BAJA NERITIC	25°	-	-	2	130	July	50	Over Shelf
NORTHERN	23°	3	122	2	40	August	80-100	Over Shelf
	22°	3	107	6	117	July/October	80-200	Edge of Shelf
CENTRAL	09°	6	11	2	1	August	80-225	Offshore
	08°	26	11	13	10	June/July /August	125-775	Offshore
	07°	6	27	9	8	May/June Aug./Sept.	175-750	Offshore
	06°	3	23	8	144	April	25	Edge of Shelf
TOTALS		47	50	42	64			

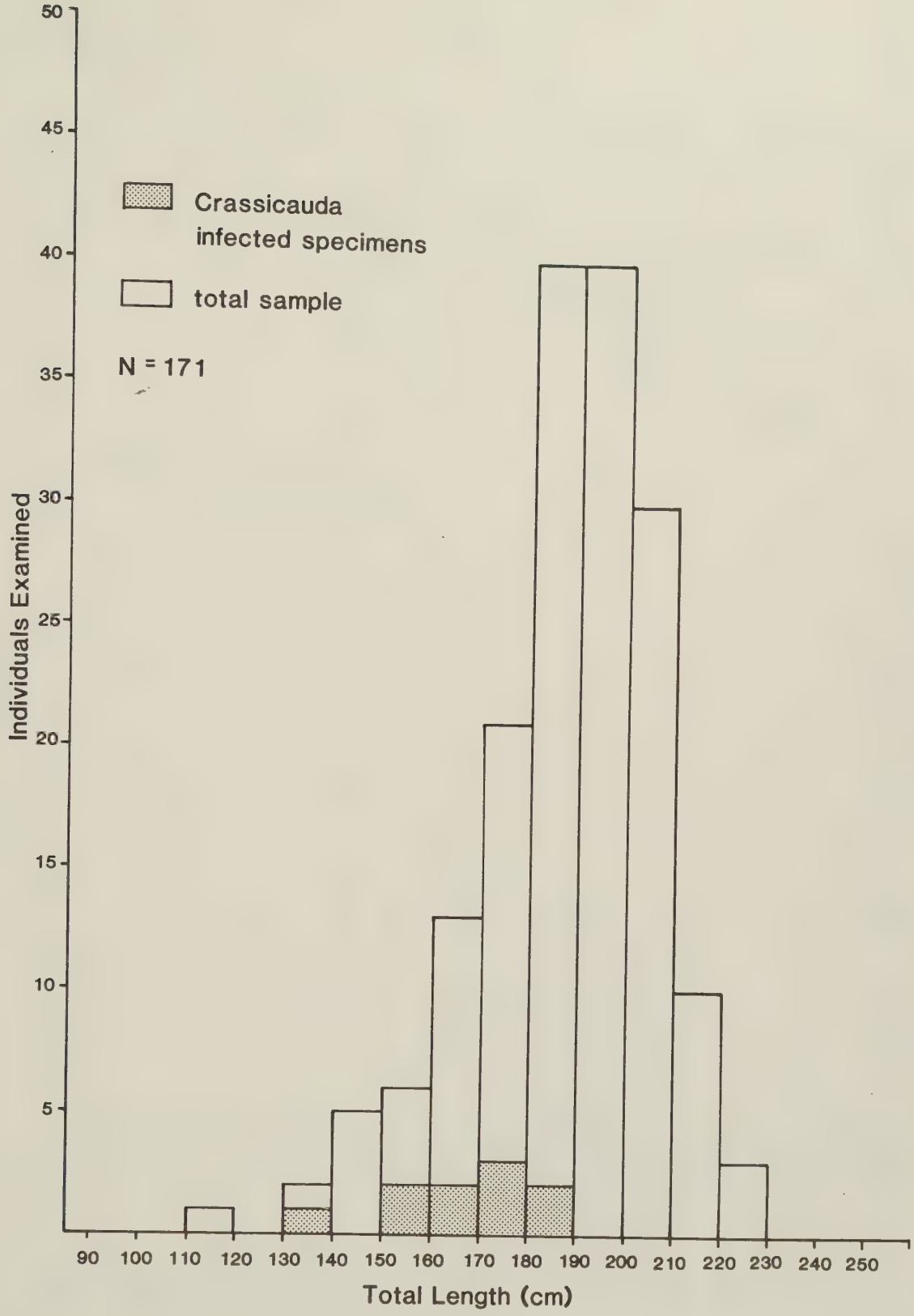

Figure 1. Length-frequency distribution of Crassicauda infected central common dolphins taken incidentally in fisheries.

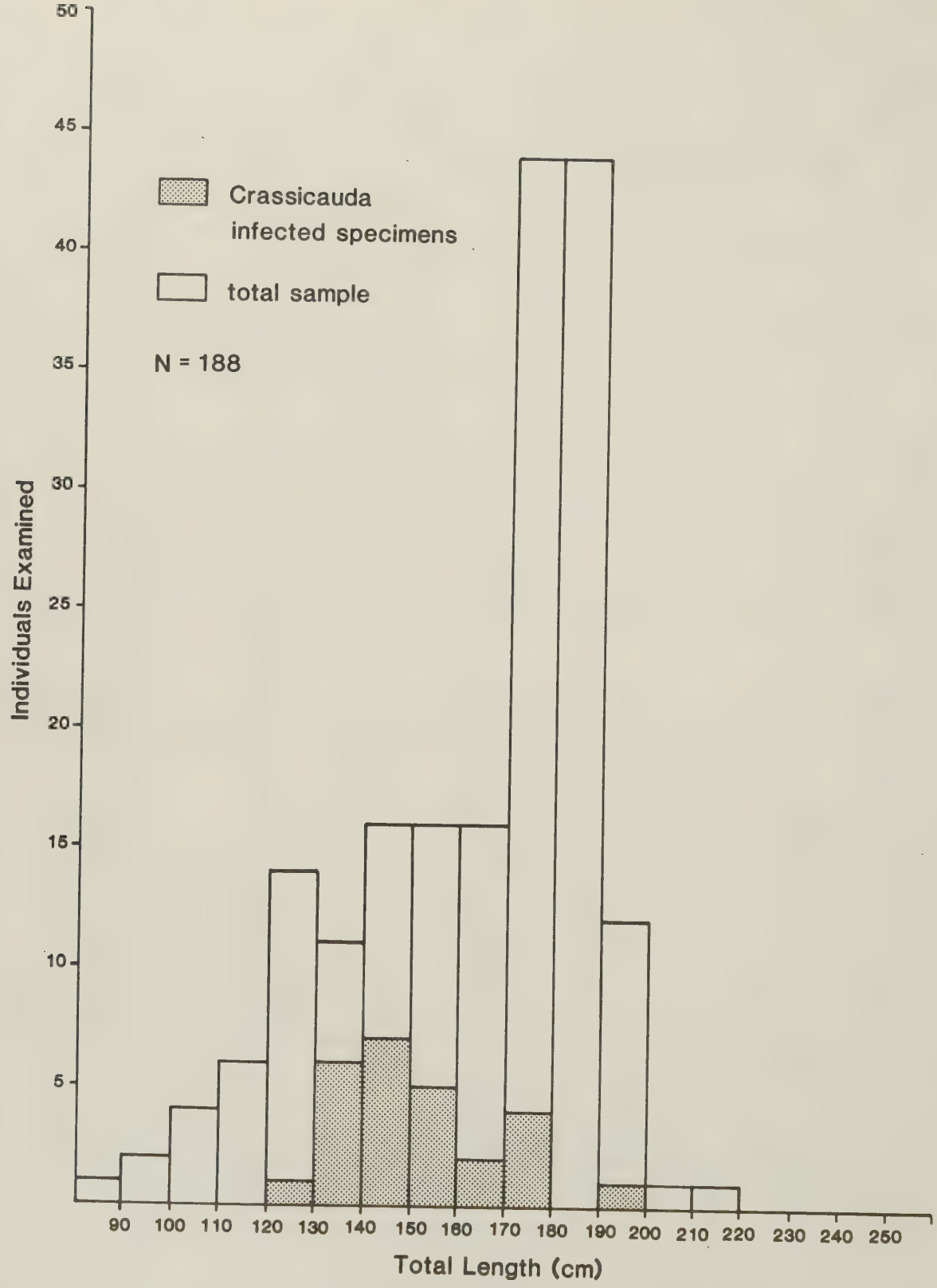

Figure 2. Length frequency distribution of Crassicauda infected northern common dolphins collected at sea.

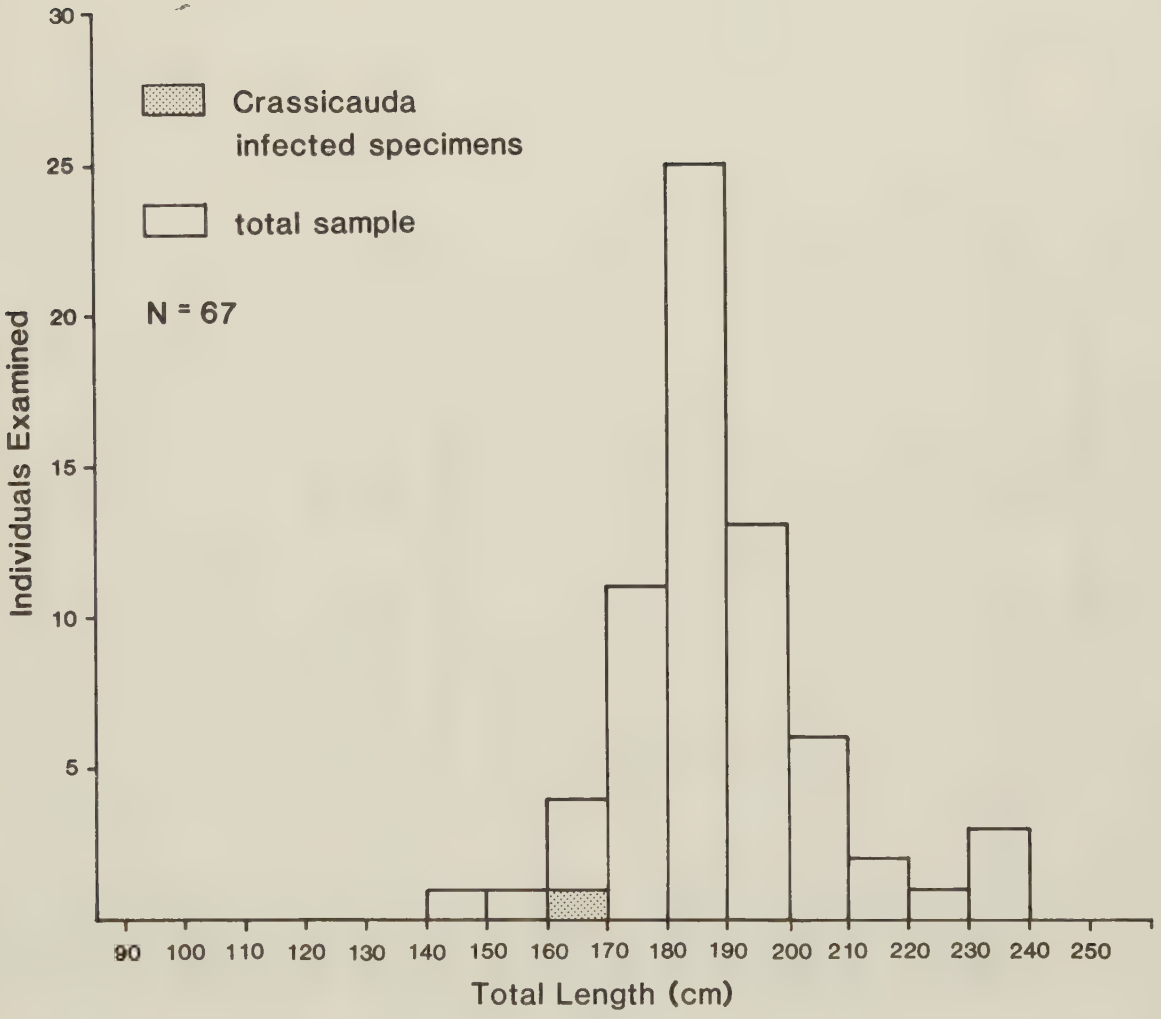

Figure 3. Length-frequency distribution of Crassicauda infected common dolphins stranded north of 32°N.

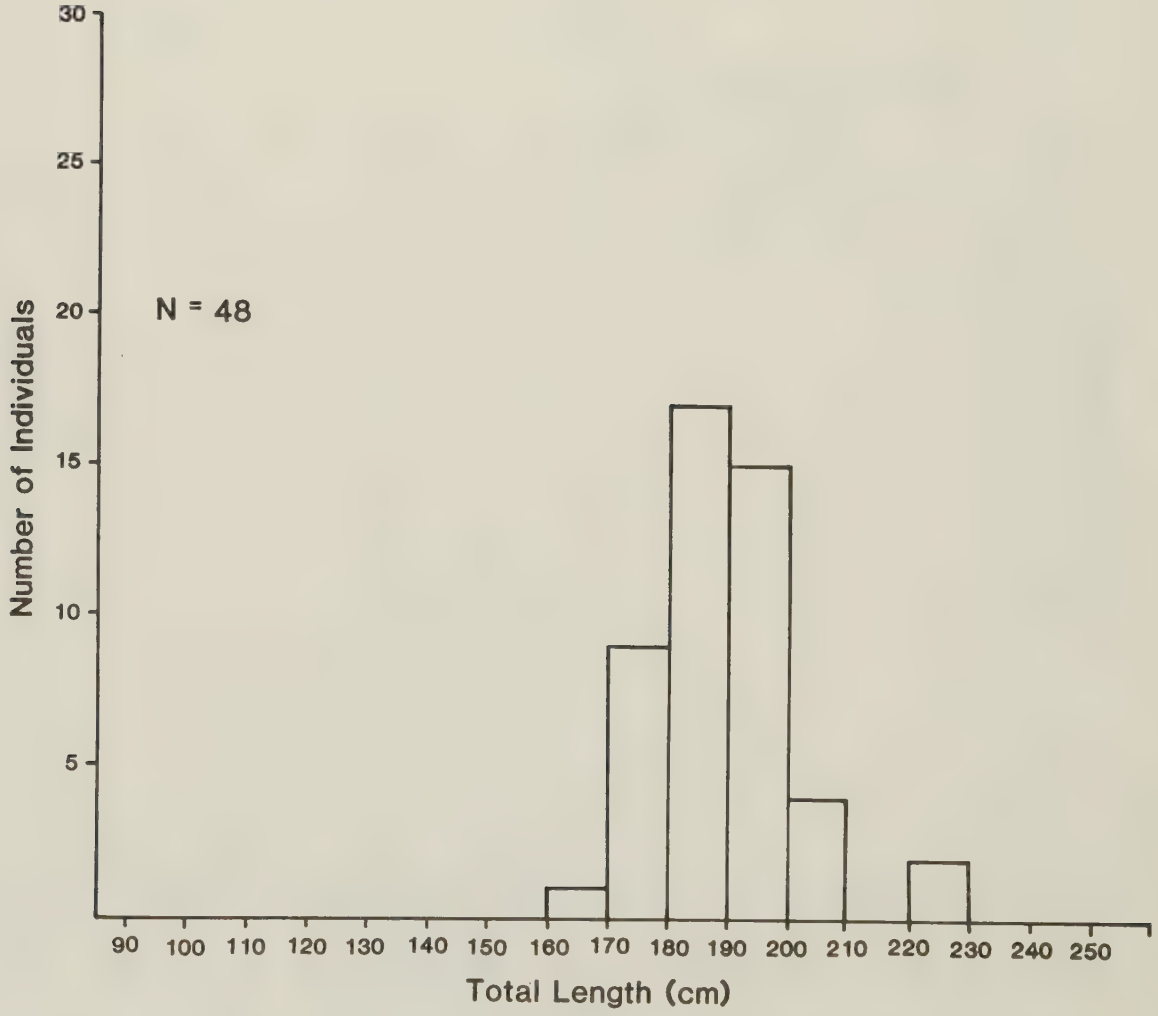

Figure 4. Length-frequency distribution of stranded common dolphins in Los Angeles County, California 1970-1974.

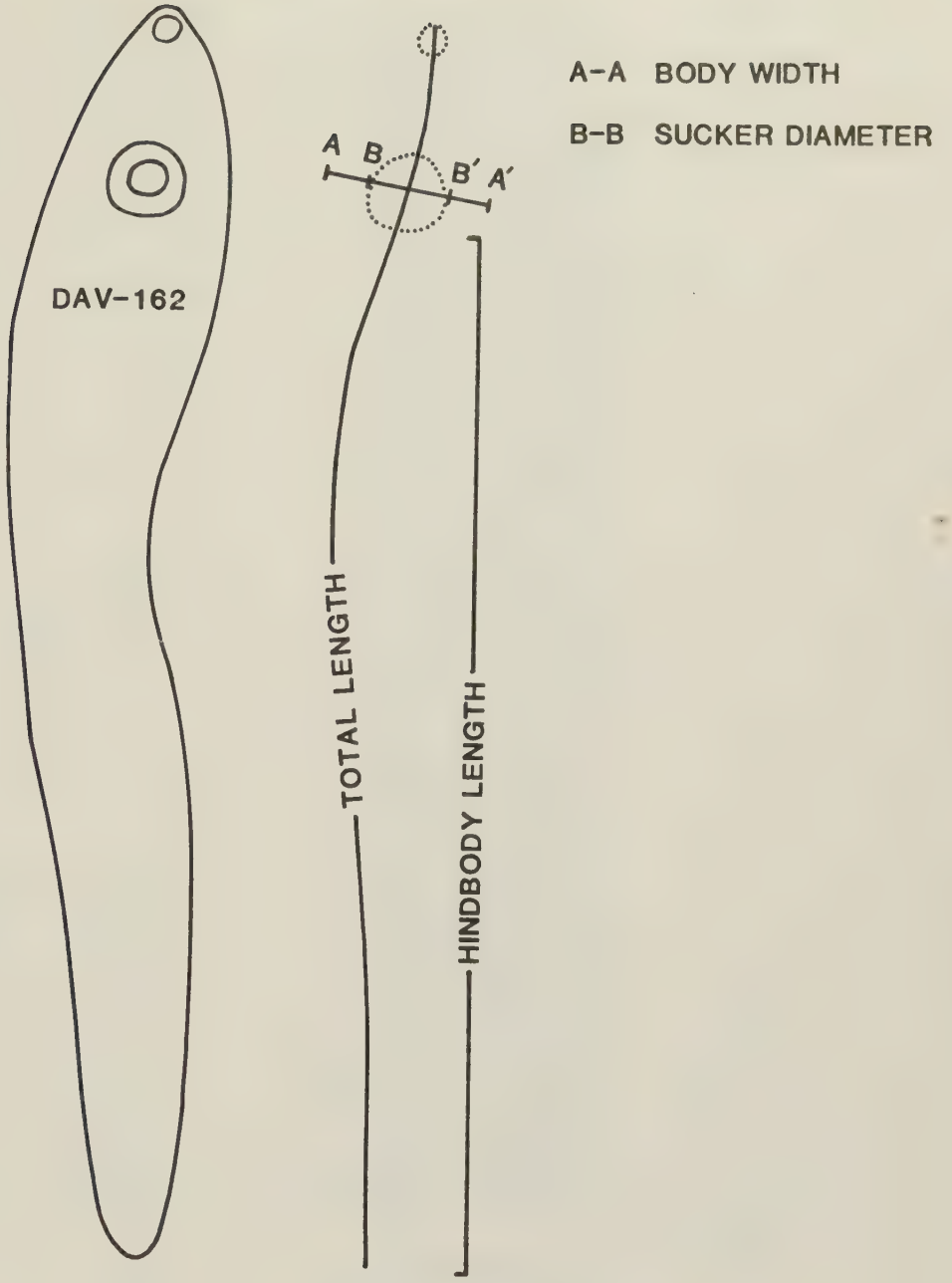

Figure 5. Measurements recorded for Nasitrema.

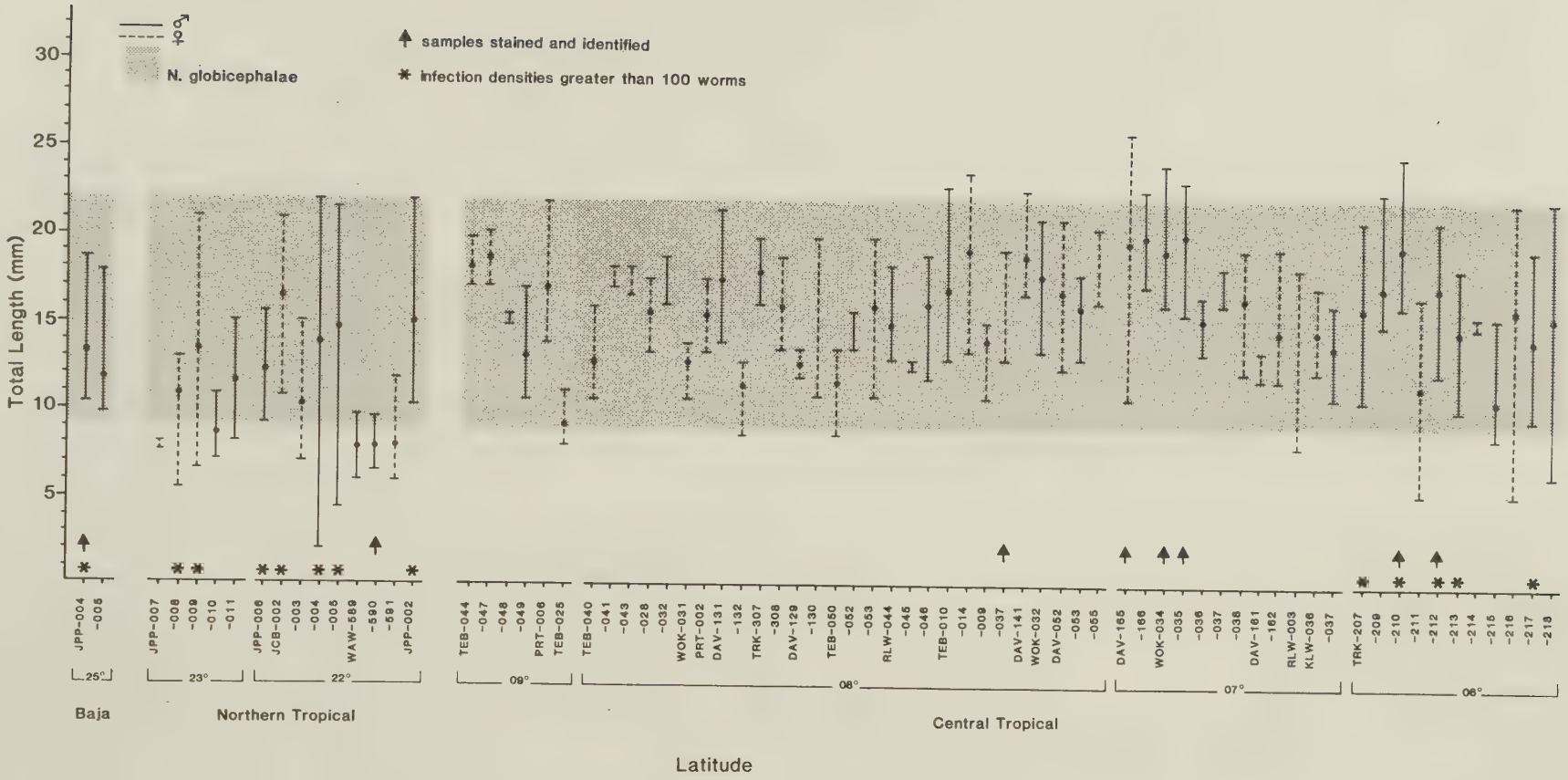

Figure 6. Size range of Nasitrema globicephalae superimposed over total lengths (ranges and means) of Nasitrema populations recovered from free-ranging common dolphins captured in the eastern North Pacific. Hosts are arranged by descending latitude and identified by sample number.

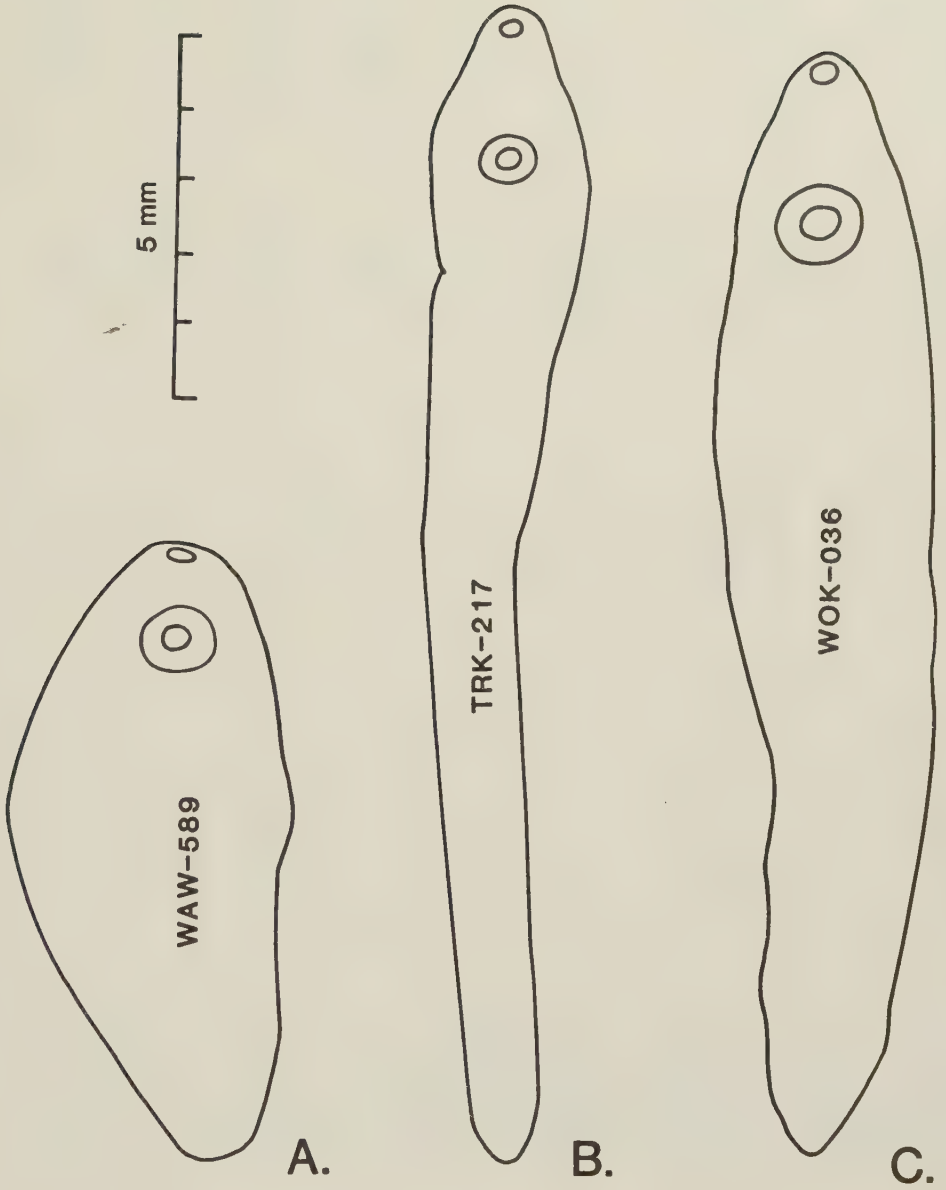

Figure 7. Nasitrema morphs observed in populations recovered from free-ranging common dolphins captured in the eastern North Pacific. Sample numbers indicated inside each drawing.

APPENDIX FREE-RANGING COMMON DOLPHINS (*DELPHINUS DELPHIS*) INFECTED WITH *NASITREMA*.

STOCK	POSITION	FIELD NUMBER	COLLECTION DATE	SEX	LENGTH	NASITREMA NO. RECOVERED / NO. MEASURED *	REMARKS
BAJA NERITIC	25°38'N; 112°35'W	JPP-004	77-07-25	M	228.0	211/10	Stain/Ident.
		JPP-005		M	182.0	49/17	
NORTHERN	23°15'N; 111°10'W	JPP-007	77-08-14	F	182.5	5/2	
		JPP-008		F	187.2	156/111	
		JPP-009		F	unk.-mature	205/155	
		JPP-010		M	186.0	9/6	
	23°10'N; 111°25'W	JPP-011	77-08-19	M	187.3	71/32	
	22°50'N; 111°20'W	JPP-006	77-08-14	M	177.3	108/69	Subsampled
	22°48'N; 110°52'W	JCB-002	77-07-10	F	167.0	203/53	Subsampled
		JCB-003		F	174.0	42/28	
		JCB-004		M	156.0	164/109	
		JCB-005		M	167.5	112/75	

* Only intact, entire worms were measured

NORTHERN (contd.)	22°16'N; 107°52'W	WAW-589	78-10-26	M	236.0	50/10	
		WAW-590		M	208.0	92/9	Stain/Ident.
		WAW-591		F	196.0	75/17	
	22°09'N; 111°52'W	JPP-002	77-07-18	M	181.0	175/124	
CENTRAL (contd.)	09°33'N; 086°19'W	TEB-044	77-08-16	F	192.0	8/4	
		TEB-045		M	191.0	1/1	Omit +
		TEB-046		F	170.0	3/2	
		TEB-047		F	190.0	10/7	
		TEB-048		M	187.0	2/2	
	09°16'N; 086°27'W	TEB-049	77-08-16	F	195.0	17/14	
	09°15'N; 087°25'W	PRT-006	77-08-06	F	167.0	10/9	
	09°10'N; 086°48'W	TEB-025	77-08-09	F	188.0	18/7	
	08°56'N; 086°19'W	TEB-040	77-08-15	F	190.0	17/12	
		TEB-041		F	181.0	3/2	
		TEB-042		F	172.0	2/1	Omit
		TEB-043		F	155.0	2/2	

+ Omitted from Figure 2

CENTRAL (contd.)	08°55'N; 086°37'W	TEB-028	77-08-09	F	170.0	11/6	
		TEB-032		M	185.0	4/2	
		TEB-034		F	170.0	2/1	Omit
		TEB-035		M	159.0	1/0	Omit
		TEB-036		F	160.0	1/1	Omit
	08°53'N; 086°27'W	WOK-030	77-07-20	M	174.0	1/1	Omit
		WOK-031		F	200.0	4/3	
	08°50'N; 087°45'W	PRT-001	77-07-24	M	197.5	1/0	Omit
		PRT-002		F	191.0	21/7	
	08°50'N; 087°04'W	DAV-131	77-08-09	M	184.0	3/0	Omit
		DAV-132		M	212.0	28/6	
		DAV-133		F	181.0	3/3	
	08°45'N; 092°20'W	TRK-307	77-07-20	M	194.0	7/4	
		TRK-308		F	197.0	29/21	
	08°25'N; 087°25'W	DAV-129	77-08-09	F	173.0	5/4	
		DAV-130		F	183.0	2/2	

CENTRAL (contd.)	08°25'N; 086°16'W	TEB-050	77-08-17	F	204.0	7/5	
		TEB-051		F	198.0	7/1	Omit
		TEB-052		M	170.0	4/2	
		TEB-053		F	178.0	5/3	
	08°22'N; 086°27'W	RLW-044	77-06-25	F	193.0	7/5	
		RLW-045		M	181.0	4/3	
		RLW-046		M	185.0	6/6	
	08°19'N; 092°36'W	TEB-010	77-07-22	M	209.0	25/18	
		TEB-013		F	194.0	1/1	Omit
		TEB-014		F	191.0	8/5	
	08°19'N; 086°48'W	TEB-009	77-07-22	F	198.0	11/6	
	08°16'N; 086°32'W	TEB-037	77-08-14	F	191.0	55/10	Stain/Ident.
	08°14'N; 086°30'W	DAV-141	77-08-13	F	193.0	78/59	
	08°11'N; 092°47'W	WOK-032	77-07-22	M	221.0	35/25	

CENTRAL (contd.)	08°10'N; 089°20'W	DAV-052	77-08-01	F	195.0	10/7	
		DAV-053		M	192.0	6/5	
		DAV-054		F	177.0	6/1	Omit
		DAV-055		F	188.0	2/2	
		DAV-058		F	183.0	1/1	Omit
	07°58'N; 087°35'W	DAV-165	77-08-21	F	193.0	65/36	Stain/Ident.
		DAV-166		M	203.0	16/9	
	07°55'N; 092°33'W	WOK-034	77-07-23	M	203.0	10/7	Stain/Ident.
		WOK-035		M	197.0	7/3	Stain/Ident.
		WOK-036		M	219.0	13/9	
		WOK-037		M	202.0	3/2	
		WOK-038		F	192.0	47/27	
	07°50'N; 087°45'W	DAV-160	77-08-21	M	215.0	3/1	Omit
		DAV-161		F	168.0	2/2	
		DAV-162		F	192.0	28/20	

CENTRAL (contd.)	07°48'N; 084°58'W	RLW-001	77-05-18	M	190.5	2/0	Omit
		RLW-002		M	182.0	11/1	Omit
		RLW-003		F	168.2	2/2	
	07°38'N; 088°33'W	KLW-036	77-09-11	F	192.0	17/8	
		KLW-037		M	167.5	9/6	
	06°55'N; 080°40'W	TRK-207	77-04-21	M	191.0	139/134	
		TRK-209		M	190.0	27/10	
		TRK-210		M	173.0	156/12	Stain/Ident.
		TRK-211		F	156.0	9/7	
		TRK-212		M	191.0	225/16	Stain/Ident.
		TRK-213		M	196.0	405/228	Subsampled
		TRK-214		F	192.0	2/2	
		TRK-215		M	206.0	17/17	
		TRK-216		F	168.0	59/35	
		TRK-217		M	200.0	149/113	
		TRK-218		M	167.0	33/23	